

## ABSTRACT

### LAKE TEMPERATURES AS SENTINEL RESPONSES TO CLIMATE CHANGE

by Rachel M. Pilla

The surface waters of two small lakes in northeastern Pennsylvania have warmed over the past 27 summers (1988-2014), but with no significant increase in air temperature, the quintessential driver of lake surface warming. I assessed long-term trends and interannual relationships between lake thermal structure and regional meteorological patterns to determine the changes in and drivers of lake temperatures. Strong increases in thermal stratification accompanied surface water warming trends in both lakes. In the clearer lake, I found cooler deepwater temperatures over time contributing to net whole-lake cooling. Precipitation significantly increased over this time period and was most strongly correlated to the changes in lake thermal structure. These changes are largely related to precipitation-driven increases in dissolved organic matter in the lakes, leading to reductions in water transparency driving thermal responses. These changes to lake ecosystems have important ecological consequences, including changes in physical processes and vertical habitat gradients.

LAKE TEMPERATURES AS  
SENTINEL RESPONSES TO CLIMATE CHANGE

A Thesis

Submitted to the  
Faculty of Miami University  
in partial fulfillment of  
the requirements for the degree of  
Master of Science  
Department of Biology

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2015

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## DEDICATION

I dedicate this work to my mother and father, Debbie and Dave, who have supported me and my love of learning all my life;

To my brothers, Gabe, Jake, Sam, and Chris, for being a great inspiration and for much-needed comedic relief over the years;

To Mason, for your unbridled love and understanding every day, and for your hot funk, cool punk – you're always rock and roll to me;

And to my grandparents, especially Grandpa Pilla, whose support, love, and words of encouragement are always with me.

## ACKNOWLEDGEMENTS

I thank my thesis advisor, Dr. Craig Williamson, for giving me this incredible research opportunity, supporting me throughout this process, and championing my goals from day one. I also thank my committee members, Dr. Mike Vanni and Dr. Jing Zhang, for their support and feedback on this work along the way. I thank my undergraduate research advisor, Dr. Stuart Jones, for introducing me to and helping me develop skills in ecology, limnology, and computing, which set the stage for me for this thesis research.

I thank the Department of Biology at Miami University, and the Global Change Limnology Research Lab. I also thank our lab manager Erin Overholt and graduate students Jennie Brentrup and Taylor Leach for feedback, logistical help, and support along the way. I thank Lacawac Sanctuary for access to Lake Lacawac and use of research facilities, and Blooming Grove Hunting and Fishing Club for access to Lake Giles. This work benefited from participation in the Global Lake Ecological Observatory Network (GLEON). I thank Bill Renwick and Ben Felzer for GIS support, climate analysis, and helpful feedback on previous versions of this manuscript. I thank Bruce Hargreaves for providing wind data from Lake Lacawac's buoy, and both Bruce Hargreaves and Nihar Samal for their helpful comments and suggestions on earlier versions of this research.

## CHAPTER 1

Long-term surface and deepwater temperature trends in two small lakes:  
A response to precipitation and dissolved organic matter rather than air temperature warming

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### ***Introduction***

Lake ecosystems are among the most effective sensors of climate change in the global landscape. Sentinel responses of lakes include responses to changes in climate, hydrology, and inputs from their terrestrial and aerial catchments and include a wide variety of physical, chemical, and biological responses with important ecological consequences (Adrian et al. 2009; Williamson et al. 2009a, 2009b, 2014). One of the most globally widespread responses of lakes to climate change is a trend of warming surface waters, which in some large lakes is about twice the rate of regional air temperature warming (Austin and Colman 2008; Hampton et al. 2008; Schneider and Hook 2010). A related response observed in many lakes is stronger thermal stratification. In a study across a range of Canadian boreal lakes, comparisons of one cool and two warm years showed not only warmer surface waters, but also shallower mixing depths and stronger thermoclines during years with warmer air temperatures (Snucins and Gunn 2000). Similarly, a study of the thermal responses of two temperate lakes in Switzerland during the European heat wave of 2003 revealed warming of the surface waters as well as strong increases in thermal stability (Jankowski et al. 2006). The global nature of these climate-driven changes in aquatic ecosystems is evident from the similar changes in thermal structure that have been observed in the world's oceans. Oceans have absorbed over 90% of the heat from climate



warming induced by anthropogenic emissions, causing warming of the ocean surface waters and increasing strength of thermal stratification (Gao et al. 2012; Sherman et al. 2013; Trenberth and Fasullo 2013).

Our observations of long-term changes in water temperature in two small temperate lakes in northeastern Pennsylvania, USA (Fig. 1) show stronger thermal stratification over the past 27 years due to warming surface waters and shallower epilimnia, as well as cooler hypolimnetic temperatures in one of the lakes (Fig. 2a, b). Warming air temperatures are widely recognized as a primary driver of thermal changes in lakes (Schneider and Hook 2010). However, during this same time period there has been no significant increase in either annually-averaged daily air temperature in the region (Fig. 2c), or air temperature averaged over the ice-free season (April through November,  $p = 0.57$ ). These observations led us to hypothesize that other climate-related forcing not related to air temperature may be driving the changes in lake thermal structure, possibly mediated by changes in water transparency.

Other studies have demonstrated that warming air temperatures are not the sole climate-related driver of changes in lake thermal structure. Changes in wind speed, solar radiation, and transparency have led to changes in thermocline depths in boreal lakes (Schindler et al. 1990). Decreasing wind velocity coupled with increasing air temperatures have led to increased stability and reduced water column mixing in Lake Tanganyika (O'Reilly et al. 2003). In contrast, increased levels of solar radiation and higher air temperatures have led to warming of the hypolimnia and deeper thermocline depths in North American boreal lakes even when there was no statistically significant trend in epilimnetic temperature (Schindler et al. 1996a). In boreal lakes, high water transparency has been observed to allow direct heating of deeper waters, suggesting an important role for water transparency in determining the nature of lake thermal response to climate change (Keller et al. 2006; Tanentzap et al. 2008; Read and Rose 2013). In many North American temperate lakes, including our two study lakes, increases in DOM (measured as the concentration and color of dissolved organic carbon, DOC) over the past 15-20 years have led to decreased lake transparency (Williamson et al. 2014), and may be an important link between lake thermal responses and climate change.

Here we use 27 years of lake temperature data from two small, temperate lakes of differing transparencies to examine the trends of nine thermal metrics and their relationships to nine meteorological variables in order to better understand the range of thermal responses that

lakes exhibit to a diverse array of meteorological forcing. We focus on metrics related to lake temperature and include buoyancy frequency as a density-based measure of stratification to compare to our temperature-based metrics of stratification. We also consider changes in the lake heat content, which can serve as a link to the underlying physical mechanisms and changes in surface heat flux that relate the climate trends to the lake thermal responses. Although changes in land-use and land cover may induce significant thermal responses in lakes (Adrian et al. 2009; Williamson et al. 2009a), there have been no changes in land-use or land cover in the watersheds of these two study lakes during the study period.

The fundamental questions that we ask here seek to relate long-term changes in lake thermal structure to significant climate drivers, with the primary goal of understanding changes in lake thermal structure over a period with no significant increases in air temperature. Specifically, we ask: 1) Which lake thermal response metric(s) have shown significant change over the study period, and thus may be the most valuable to understanding the thermal responses of lake ecosystems to climate forcing? 2) Which meteorological variable(s) show the strongest relationships to the lake thermal responses? 3) Are changes in DOM and water transparency a plausible link between climate forcing and lake thermal structure?

## ***Methods***

**Lake sampling.** Two small, temperate lakes in northeastern Pennsylvania (Fig. 1) were used to examine nine thermal sentinel response metrics (Table 1) in relation to a suite of nine meteorological variables, including individual meteorological variables and one compound metric, the Palmer Drought Severity Index (PDSI; Table 2). Lake Giles is a relatively deep (maximum depth = 23 m), transparent (average Secchi depth = 7.2 m), oligotrophic lake with low DOC concentrations ( $\sim 2.2 \text{ mg L}^{-1}$ ), and low chlorophyll concentrations ( $\sim 0.7 \text{ } \mu\text{g L}^{-1}$ ). Lake Lacawac is a shallower (maximum depth = 13 m), less transparent (average Secchi depth = 2.9 m), dystrophic lake with higher DOC concentrations ( $\sim 5.4 \text{ mg L}^{-1}$ ) and chlorophyll concentrations ( $\sim 1.7 \text{ } \mu\text{g L}^{-1}$ ). All of these water quality data represent epilimnetic averages (July–August) from 2012 to 2014. Both lakes are small seepage lakes with no substantial inlet streams. Giles has a surface area of  $0.48 \text{ km}^2$  and a retention time of 5.2 years, and Lacawac a surface area of  $0.21 \text{ km}^2$  and a retention time of 3.1 years. Both are located in basins of glacial origin with sheltered shorelines composed of mixed deciduous and coniferous forest. Lacawac's

watershed consists of 25% peat wetlands, compared to only 1.9% for Giles (Moeller et al. 1995). The higher percentage of peat wetlands surrounding Lacawac is a principal source for its darker color and higher DOC concentration than Giles.

Vertical temperature and light profiles were taken between 07 and 28 July in each lake from year to year. This time period covers a period of relatively stable mid-summer thermal stratification as well as a period when temperature profile data were most consistently available over the 27 years. Different instruments were used during these time periods, including a manual YSI 58 temperature and oxygen meter (1988-1992, measured at 1 m increments and linearly interpolated to calculate temperature at 0.2 m increments), a Biospherical Instruments (BSI) PUV 501 (1993-2002, rapid recording at 2 Hz, downcast binned at 0.2 m increments), and a BSI BIC 2104P (2003-2014, rapid recording at 4 Hz, downcast binned at 0.2 m increments). Quantitative comparison of 19 profiles over 11 years, on days when we had data from both the YSI and BSI profiles, revealed a significant difference between the readings of the two sensors at the same depth (one-sample t-test,  $p < 0.0001$ ) with no measureable effect of a time lag in the BSI profiler, so BSI profiles were offset by applying a constant of  $+0.387^{\circ}\text{C}$  to temperature profiles from 1993-2014, which did not affect metrics of depth or temperature-based stratification. In calculating the thermal response metrics (Table 1), the metalimnion was defined as the layer in which there was a  $1^{\circ}\text{C}$  or larger change per meter (Wetzel 2001). Temporary near-surface thermoclines, where stratification is intermittently present, were excluded from the seasonal thermocline by constraining the metalimnion to be  $\geq 1.2$  m in thickness. Brunt-Väisälä buoyancy frequency (hereafter “buoyancy frequency” or  $N$ ) was calculated using the rLakeAnalyzer package (Winslow et al. 2014) and converted to cycles per hour.

The rate of heat storage in each lake during the time period before the mid-July profile was calculated each year using the mid-July profile for that year and the prior temperature profile (roughly one month earlier). The median time interval between Lacawac heat content measurements was 34.5 days (min. = 25 days, max. = 47 days), and for Giles was 35 days (min. = 16 days, max. = 44 days). This time interval is long enough to resolve robust changes in heat content, while also being short enough to be indicative of the net surface heat budget during the month immediately preceding the mid-July profile (Lenters et al. 2005). The  $\sim 35$  day mean heat storage term ( $\bar{S}$ ) is calculated from

$$\bar{S} = \left( \frac{\rho_w c_w}{\bar{a}_s} \right) \sum \left( \frac{\Delta T(z)}{\Delta t} \right) \bar{a}_z \Delta z$$

where  $\rho_w$  is the density of water (1000 kg m<sup>-3</sup>),  $c_w$  is the specific heat of water (4186 J kg<sup>-1</sup> °C<sup>-1</sup>),  $a_s$  is lake surface area,  $\Delta T(z)$  is the change in temperature at each depth from June to July,  $\Delta t$  is the time interval (mean of 35 days),  $a_z$  is lake area at depth  $z$ , and  $\Delta z$  is layer thickness (1 m from 1988-1992, 0.2 m from 1993-2014).

Data on water transparency, measured as underwater photosynthetically active radiation (PAR, 400-700 nm), were collected in both lakes from 1993-2014 with the BSI PUV and BIC continuous profiling instruments and were used to determine the measured depth to which 10% of subsurface PAR penetrated at the same time as temperature profiles and using the same instruments. DOC concentrations were measured from epilimnetic water samples taken in mid-July of each year (1993-2014), filtered on ashed Whatman GF/F filters, and analyzed in a Shimadzu Total Organic Carbon Analyzer (TOC-5000 or TOC-V<sub>CPH</sub>). DOC color ( $a^*$ ) was measured as the DOC specific absorbance at 320 nm (m<sup>2</sup> (g C)<sup>-1</sup>), which is the Napierian dissolved absorption coefficient at 320 nm (m<sup>-1</sup>) divided by the DOC concentration (mg C L<sup>-1</sup>) (Williamson et al. 2014). DOC concentration and color data were not available in 2002 (Lacawac only) and 2009 (both Lacawac and Giles).

The approach that we use here involves using a single, mid-summer temperature (and corresponding light) profile as a signal of how lake thermal structure is responding to long-term changes in climate. The advantage of the approach used here is that it enables the use of older and longer-term temperature data to test for climate change signals where we do not have high-frequency data, and where mid- to late-July temperature profiles are most abundant and consistent for these two lakes. This approach uses a single annual profile collected during the same time period each year which can be used to assess long-term changes over a 27-year record, but will only detect stronger trends with a higher signal to noise ratio. Shorter-term fluctuations in weather conditions are not captured with this approach, and measurements of variability in the epilimnion temperature are particularly limiting. We directly examined the validity of this approach by comparing temperature data from high frequency thermistors (10- to 15-minute readings) in recent years in our two study lakes with the single temperature profiles taken with a manual profiling instrument. In both Lacawac and Giles, strong summer thermal stratification typically extends from late June through early September, with the maximum

occurring in late-July to early August (Fig. 3a, c). Thermistor data are available during the summer for these two lakes in 2012 (both), 2013 (Lacawac only), and 2014 (both). Using Lacawac 2012 and Giles 2014 data as contrasting lake and climate year examples, the single-sample profile was typically within two standard deviations of the mean thermistor readings from the 07-28 July sampling window (Fig. 3b, d). Variability was highest in the epilimnion, primarily in the shallow region  $< 1.2$  m related to temporary thermoclines that were excluded from our study (Fig. 3b, d). These same patterns comparing mean thermistor readings with single profiles were consistent in Lacawac 2013-2014, and in Giles 2012. As high-frequency databases increase in number and duration in the future, they will provide an even stronger analytical tool that can more fully integrate seasonal temperatures over time and reduce this noise. In the small, strongly stratified temperate lakes that we use here, and that are globally very abundant (Verpoorter et al. 2014), this approach appears to work well. In lakes with a large surface area, or lakes characterized by weak or absent thermal stratification (e.g. many Arctic, alpine, tropical, or shallow lakes), the signal-to-noise ratio is likely to be lower, and this approach less effective.

**Regional meteorological data.** Regional meteorological data were collected from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center subdivision meteorological stations, which are part of the U.S. Historical Climatology Network. Data collected at hourly to daily resolution from stations at Hawley (USC00363758; 14.8 km from Lacawac, 12.7 km from Giles) include maximum air temperature, minimum air temperature, and precipitation, and at Scranton Airport (USW00014777; 36.8 km from Lacawac, 53.4 km from Giles) include dew point and solar radiation (Fig. 1). Trends for maximum and minimum air temperatures from the Hawley station were compared with four additional NOAA meteorological stations in the region, which all confirm a lack of warming in both annually-averaged maximum and minimum air temperature over this 27-year period: Pleasant Mount (USC00367029;  $p = 0.17$ ,  $p = 0.13$ ), Port Jervis (USC00306774;  $p = 0.13$ ,  $p = 0.07$ ), Stroudsburg (USC00368596;  $p = 0.04$  ( $\tau = -0.29$ ),  $p = 0.20$ ), and Scranton Airport (;  $p = 0.32$ ,  $p = 0.36$ ). Mean daily temperature, which is not reported at a daily scale at the Hawley station, was calculated from averaging daily maximum and minimum air temperature. Thawing degree days were calculated based on daily maximum and minimum air temperature with a base temperature of  $0^{\circ}\text{C}$ . Solar radiation data at the Scranton Airport station were collected from the National Solar Radiation Database ([http://rredc.nrel.gov/solar/old\\_data/nsrdb/](http://rredc.nrel.gov/solar/old_data/nsrdb/)). Monthly PDSI data were

collected from NOAA in Pennsylvania Climate District 1 (<https://www.ncdc.noaa.gov/cag/time-series>). We used annual averages for daily data (or total in the case of precipitation) based on the previous 365-days of each year's temperature profile, inclusive of the day of sampling. For monthly data, we used a 12-month average, from 01 July of the previous year through 30 June of the sampling year.

Wind data were collected at both regional and local scales (on Lake Lacawac). We used monthly wind speed data from the ERA-Interim Reanalysis, provided by the University of Maine Climate Change Institute to represent regional wind speed near Hawley, PA, available from 1998-2013. Local daily average wind data from an on-lake buoy at Lake Lacawac were collected using an R.M. Young Co. model 05103 anemometer, available from 1993-2014 (maintained by B.R. Hargreaves, Lehigh University), and averaged to the monthly scale for comparison with ERA-Interim regional wind data. The two data sources were significantly correlated when considering each complete pair-wise month observation (Pearson  $r = 0.54$ ,  $p < 0.0001$ ), but had significantly different mean values (two-sample t-test,  $p < 0.0001$ ). On-lake wind data averaged only 54% of the regional wind mean values, reflecting the sheltered nature of Lake Lacawac due to its forested watershed and small fetch. Wind data were not available for comparison on Lake Giles, but we expected a similar pattern as observed for Lacawac as it is also forested and sheltered with a small fetch. Both regional and on-lake wind data are used independently in further analyses in this manuscript. Wind data were averaged only for the ice-free spring months (April through June), thereby excluding wind during ice cover, when the influence on summer mixing dynamics is minimal.

**Statistical analyses.** Due to non-normality and the non-linear trends of lake thermal metrics, we used Mann-Kendall non-parametric tests to assess the temporal trends for each thermal response metric in both lakes, for each meteorological variable, and for each water transparency variable in both lakes over the study period, with a significance level of  $p = 0.05$  (Mann 1945; Kendall 1975). We calculated Sen's slope to find the overall rate of the trends in lake thermal response metrics (Sen 1968).

To assess relationships between meteorological variables and lake thermal responses, we conducted univariate Kendall non-parametric Tau tests of the nine meteorological variables vs. each of the nine lake thermal response metrics per lake, with a significance level of  $p = 0.05$ . Since changes in DOC and water transparency are well known to control thermal responses in

lakes (Keller et al. 2008; Read and Rose 2013), we assessed if water transparency was a plausible link of changes in lake thermal structure. We conducted Kendall non-parametric Tau tests of lake-specific 10% PAR depth vs. each of the nine thermal response metrics, with a significance level of  $p = 0.05$ . We used 10% PAR depth because it reflects both the concentration and color ( $a^*$ ) of DOC in the lakes as a single measure of water transparency. All analyses were completed in R (versions 2.15.2 and 3.0.2; R Core Team 2014) using the “Kendall” (McLeod 2011) and “rLakeAnalyzer” (Winslow et al. 2014) packages.

## Results

**Trends in thermal response metrics.** The strongest trends in thermal response metrics were increases in the strength of thermal stratification, with Lake Giles consistently showing stronger trends than Lake Lacawac for all thermal metrics.  $T_E$  increased significantly in Giles during the study period at a rate of  $0.12^\circ\text{C yr}^{-1}$  ( $p < 0.001$ ; Fig. 4a), and also in Lacawac, at a rate of  $0.09^\circ\text{C yr}^{-1}$  ( $p = 0.03$ ; Fig. 4a).  $T_H$  decreased significantly in Giles at a rate of  $-0.14^\circ\text{C yr}^{-1}$  ( $p < 0.001$ ; Fig. 4b), and generally decreased, though not significantly, in Lacawac at a rate of  $-0.05^\circ\text{C yr}^{-1}$  ( $p = 0.06$ ; Fig. 4b).  $T_H$  in July of 1988 was extremely cool in both lakes throughout the spring and summer, but these extreme values early in the study period did not affect the significance of the long-term trend (or lack thereof in Lacawac).  $T_W$  significantly decreased in Giles at a rate of  $-0.08^\circ\text{C yr}^{-1}$  ( $p < 0.01$ ; Fig. 4c), but did not significantly change in Lacawac ( $p = 0.90$ ; Fig. 4c).  $\bar{S}$ , which considers the change in volumetric whole-lake temperature from mid-June to mid-July (see above, Fig. 4c), showed a slight but statistically insignificant downward trend for Lake Giles ( $p = 0.07$ ; Fig. 4d), and did not show a significant trend for Lake Lacawac ( $p = 0.56$ ; Fig. 4d). However, the difference in heat storage rates between Giles and Lacawac did show a significant decrease ( $p = 0.02$ ), with the difference approaching zero, indicating that the overall surface energy balances of the two lakes have become more similar through time. Of the two depth metrics,  $Z_E$  decreased significantly in Giles at a rate of  $-0.11 \text{ m yr}^{-1}$  ( $p < 0.0001$ ; Fig. 4e), but showed no significant trend in Lacawac ( $p = 0.46$ ; Fig. 4e).  $Z_M$  showed no significant trend in either Giles or Lacawac ( $p = 0.92$ ,  $p = 0.60$ , respectively; Fig. 4f). All three metrics of thermal stratification significantly increased in both lakes:  $T_E - T_H$  at a rate of  $0.23^\circ\text{C yr}^{-1}$  in Giles ( $p < 0.0001$ ; Fig. 4g) and  $0.11^\circ\text{C yr}^{-1}$  in Lacawac ( $p = 0.04$ ; Fig. 4g);  $\Delta_M$  at a rate of  $0.03^\circ\text{C m}^{-1} \text{ yr}^{-1}$  in both Giles and Lacawac ( $p < 0.001$ ,  $p < 0.01$ , respectively; Fig. 4h); and  $N$  at a rate of  $1.73$

cph yr<sup>-1</sup> in Giles ( $p < 0.0001$ ; Fig. 4i) and 0.81 cph yr<sup>-1</sup> in Lacawac ( $p < 0.001$ ; Fig. 4i). For all thermal response metrics in both lakes, residual analyses of temporal trends showed no significant temporal autocorrelation.

**Trends in meteorological variables.** Of the meteorological variables, precipitation showed a significant increasing trend over time ( $p = 0.01$ ; Fig. 5a). The compound PDSI showed a slight, but not statistically significant increase over time ( $p = 0.07$ ; Fig. 5b), indicating a trend toward wetter conditions in recent years. No significant trends were found in mean, maximum, or minimum air temperature ( $p = 0.71$ ,  $p = 0.68$ ,  $p = 0.26$ , respectively; Fig. 2c), solar radiation ( $p = 0.60$ ; Fig. 5c), thawing degree days ( $p = 0.65$ ; Fig. 5d), wind speed (regional wind  $p = 0.66$ , on-lake wind  $p = 0.09$ ; Fig. 5e), or dew point ( $p = 1$ ; Fig. 5f).

**Trends in water transparency.** DOC concentration significantly increased in Giles during the study period ( $p < 0.0001$ ; Fig. 6a), and has generally increased in Lacawac, though not significantly ( $p = 0.07$ ; Fig. 6a). DOC-specific absorbance ( $a^*$ , DOC color) significantly increased in Giles ( $p < 0.001$ ; Fig. 6b), but not in Lacawac ( $p = 0.11$ ; Fig. 6b). Water transparency measured as 10% PAR depth significantly decreased in both lakes (Giles  $p < 0.0001$ , Lacawac  $p = 0.04$ ; Fig 6c). In both Lacawac and Giles, profiles taken from approximately mid-June show no significant trend in volumetric whole-lake temperature over the 27 years (Giles  $p = 0.56$ , Lacawac  $p = 0.45$ ; Fig. 6d).

**Relationships between thermal response metrics and meteorological variables.** In addition to the long-term trends, lake thermal response metrics in both lakes were most strongly correlated with precipitation and the related PDSI. In Giles, precipitation was positively related to stratification ( $T_E - T_H$  and  $\Delta_M$ ), and negatively related to  $T_H$  and  $Z_E$  (Table 3). Giles  $N$  was significantly negatively associated with wind speed,  $T_W$  was positively associated with minimum air temperature, and  $\bar{S}$  was positively associated with both solar radiation and PDSI (Table 3). In Lacawac, precipitation was negatively associated with  $T_W$  and  $Z_E$ , and positively with  $T_E$  and the two stratification metrics  $T_E - T_H$  and  $N$ , while  $\Delta_M$  was positively associated with PDSI (Table 3). Lacawac  $T_W$  was also significantly related to dew point (Table 3).

Lake thermal response metrics showed stronger correlations with water transparency (10% PAR depth) than with meteorological variables in many cases, particularly in Giles. In Giles, all metrics of thermal stratification ( $T_E - T_H$ ,  $\Delta_M$ , and  $N$ ) were negatively related to 10% PAR depth, and  $T_H$ ,  $Z_E$ , and  $T_W$  were positively related to 10% PAR depth (Table 4). In Lacawac,



$Z_E$  and  $T_W$  were positively associated with 10% PAR depth (Table 4).

## ***Discussion***

Increases in surface water temperature and thermal stratification are two of the most pervasive changes that are being observed in lakes and oceans in response to climate change (Hampton et al. 2008; Schneider and Hook 2010; Gao et al. 2012; Trenberth and Fasullo 2013). These responses are often attributed to warming air temperature, yet in our study lakes we observed these same two responses with no significant increases in regional air temperature or other temperature-related meteorological variables. Surface warming and increased strength of stratification in these study lakes were strongly related to increases in precipitation and corresponding decreases in water transparency. This indicates that lakes are valuable sentinels of climate forcing beyond just changes in air temperature-related meteorological variables.

The mechanism involved here likely consists of decreased transparency that leads to trapping more heat near the surface and reducing the heating of the hypolimnion. This in turn leads to warming of surface waters, cooling of the hypolimnion, stronger thermal stratification, and reduced vertical heat transfer among lake strata. Consistent with this mechanism, the three metrics of thermal stratification that are the result of both warming of surface waters and cooling of deep waters showed strong increases over time. This suggests that in some lakes climate-change induced increases in precipitation are augmenting the thermal responses of lakes to warmer air temperatures and may contribute to the widely observed greater increases in lake surface water temperatures compared to regional air temperatures (Schneider and Hook 2010; Austin and Colman 2008).

The patterns observed in both of our study lakes are also consistent with other studies that link two or more of these components (precipitation, DOC, and transparency) to changes in lake thermal structure. For example, increases in precipitation are related to increased DOC concentration and color in lakes (Zhang et al. 2010; Jennings et al. 2012), including both Lacawac and Giles (Williamson et al. 2014). These observed increases in DOC concentration and/or color were coincident with reduced water transparency. Similarly, decreases in transparency have been reported to strengthened thermal stratification (Keller et al. 2006; Tanentzap et al. 2008; Read and Rose 2013), and lead to a reduction in the depth of the epilimnion (Schindler 1990; Houser 2006; Fortino et al. 2014) as we observed in our lakes,

particularly in Lake Giles. Each of these relationships is consistent with a number of observational and modelling studies showing increases in DOC leading to stronger thermal stratification (Gunn et al. 2001; Stasko et al. 2012; Read and Rose 2013), as well as long periods of drought leading to decreased DOC inputs and deeper thermoclines (Schindler et al. 1996a, 1996b; Schindler et al. 1997). These prior studies support our hypothesized mechanism relating precipitation, water transparency, and lake thermal structure in Lacawac and Giles

These links between precipitation, increased DOC concentration and color, reduced water transparency, and thermal structure have been observed across multiple time scales in other diverse lake types. For example, in alpine Emerald Lake in California, a single storm event delivered a quantity of DOC similar to the total annual inputs to the lake and decreased water transparency by more than three-fold, increasing the thermal stratification (Sadro and Melack 2012). In subtropical Lake Annie in Florida, regional forcing of precipitation events by the Atlantic Multidecadal Oscillation have been linked to fluctuations in water color over 30-year cycles (Gaiser et al. 2009a), with corresponding changes in the depth of the thermocline (Gaiser et al. 2009b).

The decrease in Lake Giles's volumetric whole-lake temperature is consistent with reduced transparency leading to a warmer and shallower epilimnion and a cooler hypolimnion that is increasing in volume. The "thinning" of the epilimnion in Lake Giles is a result of greater light absorption at the surface, and consequently reduced penetration of solar radiation to the deeper strata, which leads to a net cooling effect of the whole lake despite the warming surface waters. The warming and shallowing of the epilimnion enhances heat loss at the surface. Since air temperature trends are absent, there is a greater temperature gradient between the lake and the air. Warmer surface water alone will lead to increases in evaporation, positive-upward (i.e., lake-to-air) sensible and latent heat fluxes, and increases in loss of longwave radiation from the lake surface waters, each of which contribute to the declining summer heat content and heat storage rate for Lake Giles (Houser 2006). Lake Lacawac, with already high DOC and low transparency, has experienced little or no change in either summer heat content or heat storage rate, and reflects a lake that has already-high light attenuation such that no substantial amount of solar heating took place in the deeper strata even in the early study years. Across lakes, such differences in transparency may explain in part why deep waters of some small lakes are cooling while in other presumably clearer lakes, the deep waters are warming (Winslow et al. 2015).

Clear, low-DOC lakes such as Giles appear to be more sensitive to DOC increases than less transparent lakes. For nearly all trends in lake thermal and transparency variables, Giles is changing more rapidly than Lacawac. This stronger response of a clearer lake to climate forcing is consistent with what has been found in temperate lakes in Canada, wherein more transparent lakes show a heightened sensitivity to small changes in hydrologic inputs that influence transparency and other physical characteristics (Snucins and Gunn 2000). Thus, more transparent lakes may be optimal systems to study further ecological consequences of climate change. The complement to this is that less transparent lakes are better buffered from climate change, specifically precipitation-induced changes in transparency and therefore may experience less severe thermal changes and resulting ecological consequences (Read and Rose 2013).

Wind is often considered to be a dominant driver of the physical structure of lakes, but we found that it was not a major driver of thermal structure in our two small study lakes. The significant relationship between wind and buoyancy frequency in Giles was the only sign of the influence of wind on thermal structure, and the relationship signals higher wind speeds lead to less thermal stability, which is consistent with the well-known effects of wind, typically in larger lakes (Fee et al. 1996; O'Reilly et al. 2003; Read et al. 2012). Wind was overall not a dominant driver in these two small lakes, but may be important at shorter time scales or during extreme wind events (Klug et al. 2012). However, in larger lakes such as Tanganyika, where wind is a primary driver of mixing and thermal structure, changes in wind patterns may be very important in understanding the lake thermal structure (O'Reilly et al. 2003). The effect of wind is largely dependent on the surface area, fetch, and sheltering of the lake (Fee et al. 1996; Markfort et al. 2010; Read et al. 2012). In Lacawac and Giles, the small surface area and sheltering from the surrounding forest limit wind action on the lake surface, and convective mixing from nocturnal heat loss is likely a more important mechanism for vertical heat transfer (Smyth 2010; Read et al. 2012; Winslow et al. 2015). With nighttime (minimum) temperatures increasing faster than daytime temperatures globally (IPCC 2013), nocturnal heat loss and convective mixing in small lakes may decline, suggesting further increases in strength of stratification.

Though increasing precipitation was the dominant process affecting these lake thermal responses, increasing air temperatures may become more important in these lakes in the future. Climate change projections in this region predict both warmer air temperatures and significant increases in the amount of precipitation and frequency of storm events (IPCC 2013; Melillo et al.

2014). These warmer and wetter conditions will likely combine to drive increases in thermal stratification in small lakes that are not dominated by wind forcing, leading to a compounded increase in lake thermal stratification through both temperature- and precipitation-mediated processes (Fig. 7). In larger lakes (> 500 ha) and oceans precipitation-driven changes in transparency are likely to be less important than warmer air temperatures or changes in wind in driving thermal structure (Fee et al. 1996; Read et al. 2012). Further studies that include hydrologic, phenology, and DOC color data are needed to elucidate the multiple mechanisms that underlie the relationship between climate change and lake thermal responses.

The ecological consequences of increased thermal stratification include changes in physical processes, alteration of the vertical habitat gradient, and the availability of temperature optima, food, and predator-free habitats, particularly for temperature-sensitive organisms. Stronger thermal stratification increases water column stability and reduces vertical mixing and nutrient upwelling, while increases in DOC and reductions in transparency reduce light availability for both visual predation and primary productivity at deeper depths (Sobrino et al. 2009; Gao et al. 2012; Jones et al. 2012). Reduced mixing may also create a greater potential for anoxia in the hypolimnion, increase internal phosphorus loading, and promote methane production (Marotta et al. 2014). During the European heat wave of 2003, for example, one of two Swiss study lakes exhibited a severe increase in strength of stratification and subsequent oxygen depletion (the other was already anoxic before the heat wave; Jankowski et al. 2006). Cooler hypolimnetic waters with low oxygen concentrations have been shown to slow mineralization rates of organic matter, and thus heighten carbon storage and burial in sediments (Fortino et al. 2014). Modeling efforts combined with in situ lake measurements from 65 central European lakes have shown that shallower mixing depths are associated with higher algal and zooplankton biomass per area, which can enhance food resources for higher trophic levels (Berger et al. 2006). However, in Lake Tanganyika, the observed increases in thermal stability and decreased mixing have led to reduced nutrient supply and decreased lake productivity, with critical implications for fish populations and food supply for the region (O'Reilly et al. 2003). Temperature and stratification changes can have particularly important implications for thermal habitats, including vertical distribution and vertical migration of *Daphnia* (Williamson et al. 2011), fish habitat availability, and changes in predator-prey overlap (De Stasio et al. 1996). Further, phenology of ecosystem interactions may become uncoupled due to climate-induced

changes in lake physical structure, which may become more pronounced and have cascading effects throughout the ecosystem (Walther et al. 2002; Winder & Schindler 2004).

We conclude that the changes in lake thermal structure identified in this study are largely a response to increases in precipitation, mediated by reductions in transparency, rather than a response to regional air warming or other temperature-based variables. Further studies are needed to examine the responses of lakes with a wide variety of characteristics (e.g. DOC, transparency, latitude, altitude, size, etc.) and across regional to continental and global scales where climate regimes and climate change projections differ widely, thus affecting the lake thermal responses. The potentially greater sensitivity of clear lakes to climate change may also help identify sentinel lakes that can contribute new insights into thermal responses and the corresponding ecological response of terrestrial as well as aquatic ecosystems to both temperature and precipitation components of our changing climate.

## TABLES

**Table 1.** Thermal response metrics measured in this study, with abbreviations, descriptions, and units. Response metrics are grouped according to whether they are measures of temperature and heat, depth, or thermal stratification.

Thermal Response Metrics	Description	Units
Temperature and Heat Metrics		
Mean epilimnion temperature ( $T_E$ )	mean temperature from 0 m to the bottom of the epilimnion (top of $\geq 1^\circ\text{C m}^{-1}$ change)	$^\circ\text{C}$
Mean hypolimnion temperature ( $T_H$ )	mean temperature from top of the hypolimnion (bottom of $\geq 1^\circ\text{C m}^{-1}$ change) through the deepest measurement	$^\circ\text{C}$
Whole-lake temperature ( $T_W$ )	volumetric whole-lake temperature	$^\circ\text{C}$
Heat Storage Rate ( $\bar{S}$ )	one month (approx.) rate of heat storage (see detailed explanation in Methods)	$\text{W m}^{-2}$
Depth Metrics		
Epilimnion depth ( $Z_E$ )	distance from 0 m to the bottom of the epilimnion (top of $\geq 1^\circ\text{C m}^{-1}$ change)	m
Metalimnion thickness ( $Z_M$ )	distance from the top to the bottom depths where $\geq 1^\circ\text{C m}^{-1}$ temperature change occurs	m
Stratification Metrics		
Epilimnion-Hypolimnion temperature range ( $T_E - T_H$ )	difference between $T_E$ and $T_H$	$^\circ\text{C}$
Metalimnion slope ( $\Delta_M$ )	difference between the $T_E$ and $T_H$ divided by $Z_M$	$^\circ\text{C m}^{-1}$
Buoyancy frequency ( $N$ )	buoyancy frequency of the seasonal thermocline	cph

**Table 2.** Description and units for meteorological variables. For daily data, we used a 365-day average inclusive of the day of sampling. For monthly data, we used a 12-month average, from 01 July of the previous year through 30 June of the sampling year.

<b>Meteorological Variable</b>	<b>Description</b>	<b>Units</b>
Maximum air temperature	Daily maximum air temperature, averaged over 365 days	°C
Minimum air temperature	Daily minimum air temperature, averaged over 365 days	°C
Mean air temperature	Mean of daily maximum and minimum air temperatures, averaged over 365 days	°C
Precipitation	Daily precipitation plus water equivalent of snow, summed over 365 days	cm yr <sup>-1</sup>
Palmer Drought Severity Index (PDSI)	Monthly PDSI values, averaged over 12 months (negative values indicate drought conditions)	n/a
Solar radiation	Daily-averaged hourly solar radiation, averaged over 365 days; data n/a for 2011-2014	W m <sup>-2</sup>
Thawing Degree Days (TDD)	Sum of total degree days with temperature base 0°C, summed over 365 days	degree days
Dew point	Daily-averaged hourly dew point, averaged over 365 days	°C
Wind speed (spring)	Monthly-averaged April, May, June wind speed; data n/a for 2014 for regional station; data n/a for 1988-1992 for on-lake buoy station	m s <sup>-1</sup>

**Table 3.** Tau coefficients from individual Kendall rank correlation non-parametric tests for all meteorological variables vs. all lake thermal response metrics in Lake Giles and Lake Lacawac. Meteorological variables and Tau coefficients are reported for all significant correlations ( $p < 0.05$ ). “n/a” denotes that no correlation was significant for a given thermal metric. Note that the two sources of spring wind data (regional vs. on-lake) were treated independently.

<b>Thermal Response Metric</b>	<b>Giles Meteorological Variable (<math>\tau</math> coefficient)</b>	<b>Lacawac Meteorological Variable (<math>\tau</math> coefficient)</b>
$T_E$	n/a	Precipitation (0.29)
$T_H$	Precipitation (-0.30)	n/a
$T_W$	Min. air temperature (0.31)	Precipitation (-0.30); Dew Point (0.28)
$\bar{S}$	Solar Radiation (-0.34); PDSI (-0.28)	n/a
$Z_E$	Precipitation (-0.32)	Precipitation (-0.33)
$Z_M$	n/a	n/a
$T_E - T_H$	Precipitation (0.29)	Precipitation (0.35)
$\Delta_M$	Precipitation (0.39)	PDSI (0.40)
$N$	Wind (on-lake; -0.33)	Precipitation (0.35)

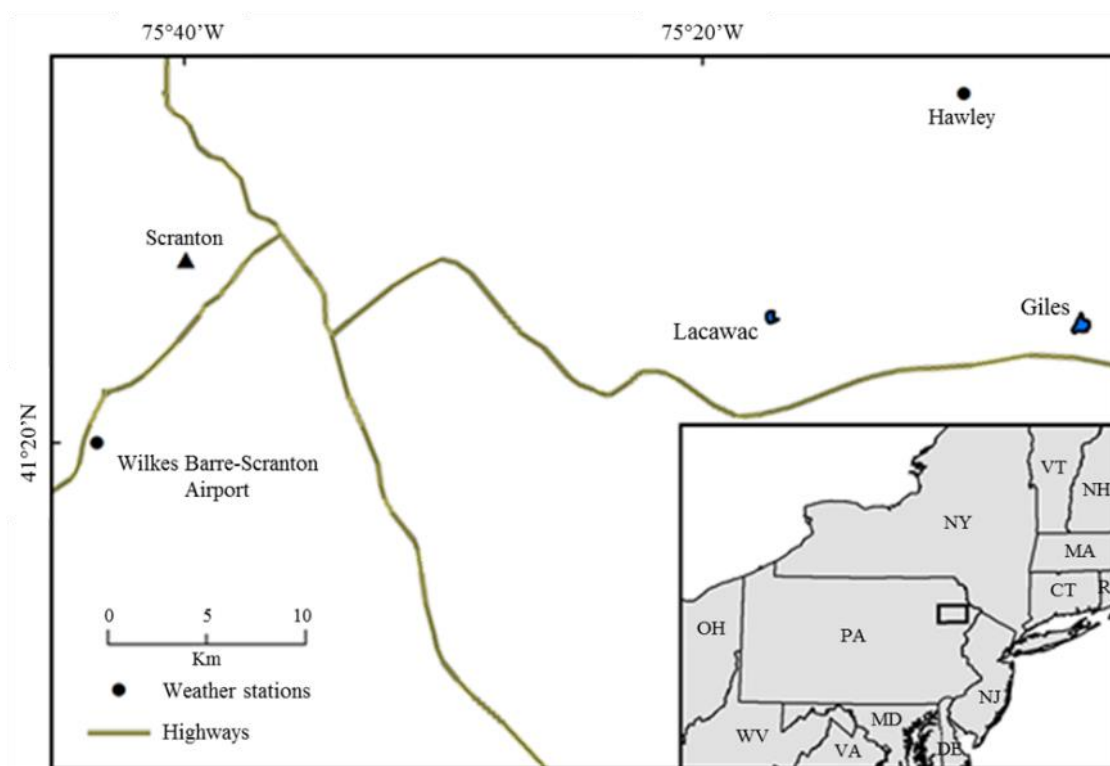


**Table 4.** Tau coefficients and  $p$ -values from Kendall rank non-parametric tests of lake-specific 10% PAR depth vs. all lake thermal response metrics in Giles and Lacawac. Tau coefficients with significant  $p$ -values ( $p < 0.05$ ) are in bold.

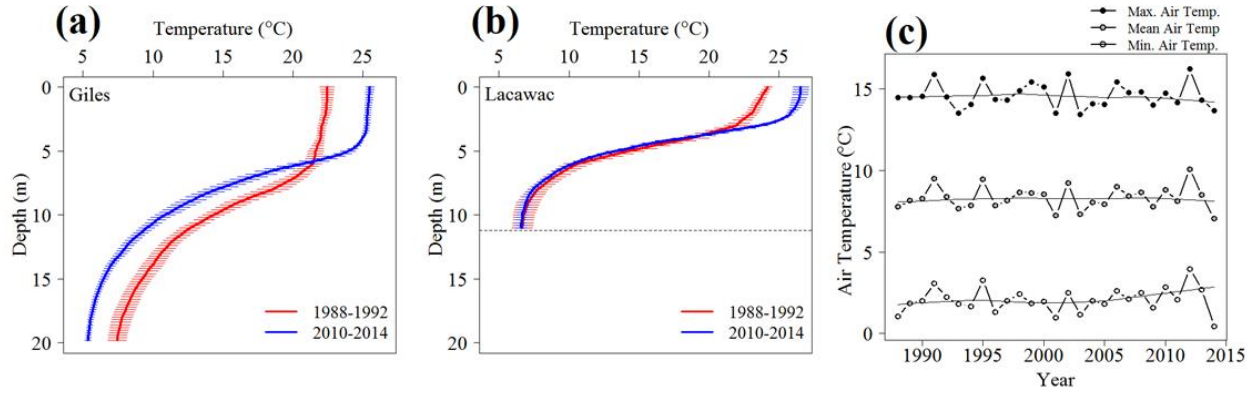
<b>Thermal Response Metric</b>	<b>Giles</b>		<b>Lacawac</b>	
	<b><math>\tau</math> coefficient</b>		<b><math>\tau</math> coefficient</b>	
	<b>(<math>p</math>-value)</b>		<b>(<math>p</math>-value)</b>	
$T_E$	-0.29	(0.06)	-0.06	(0.69)
$T_H$	<b>0.54</b>	<b>(&lt; 0.001)</b>	0.19	(0.24)
$T_W$	<b>0.64</b>	<b>(&lt; 0.0001)</b>	<b>0.50</b>	<b>(&lt; 0.01)</b>
$\bar{S}$	0.30	(0.06)	-0.27	(0.08)
$Z_E$	<b>0.64</b>	<b>(&lt; 0.0001)</b>	<b>0.53</b>	<b>(&lt; 0.01)</b>
$Z_M$	0.06	(0.71)	-0.12	(0.48)
$T_E - T_H$	<b>-0.55</b>	<b>(&lt; 0.001)</b>	-0.13	(0.43)
$\Delta_M$	<b>-0.57</b>	<b>(&lt; 0.001)</b>	-0.05	(0.78)
$N$	<b>-0.52</b>	<b>(&lt; 0.001)</b>	-0.19	(0.24)

## FIGURES

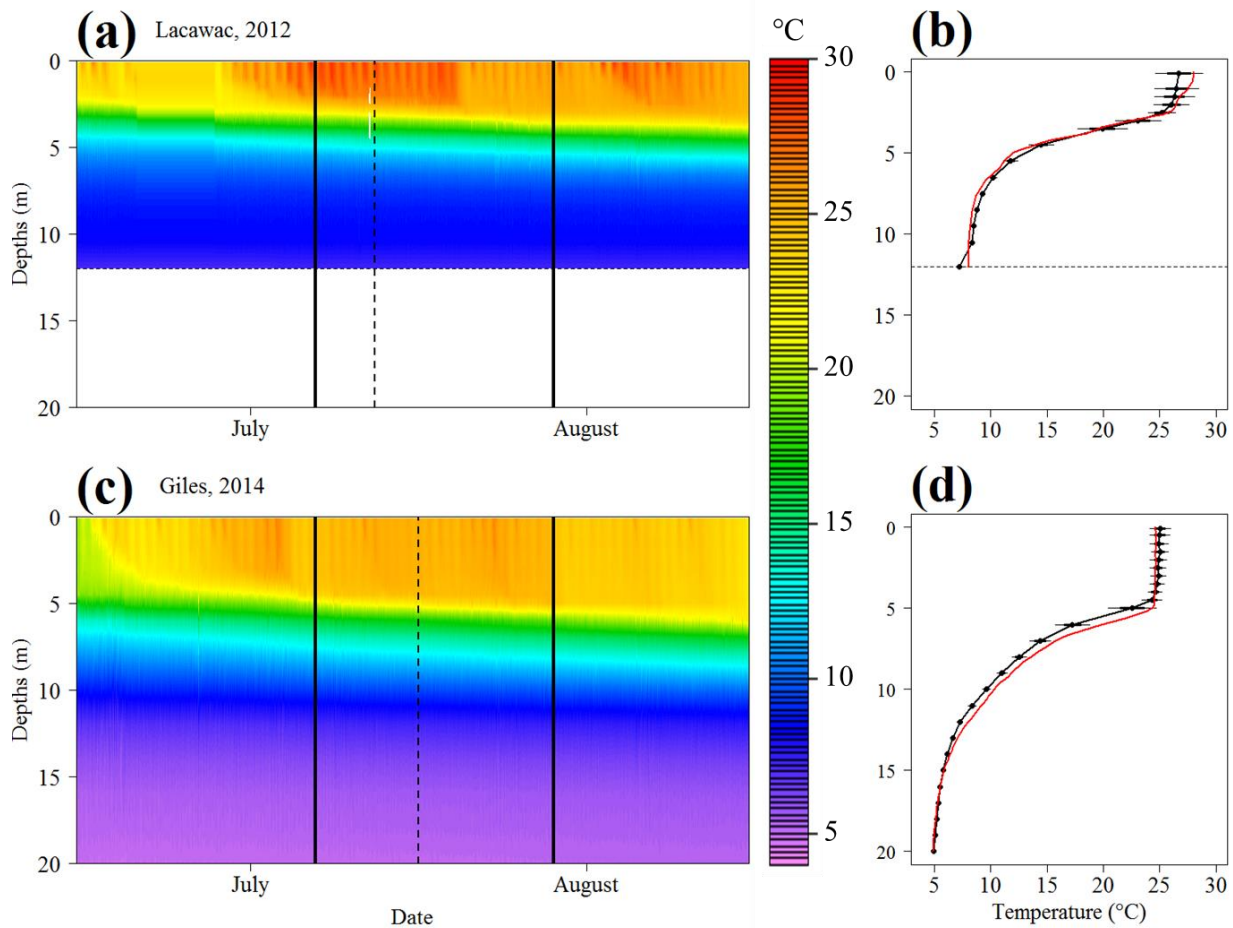
**Figure 1.** Locations of Lake Lacawac and Lake Giles in northeastern Pennsylvania. The direct distance between the two lakes is approximately 17 km. Both the Hawley and Wilkes Barre-Scranton Airport meteorological stations are shown.



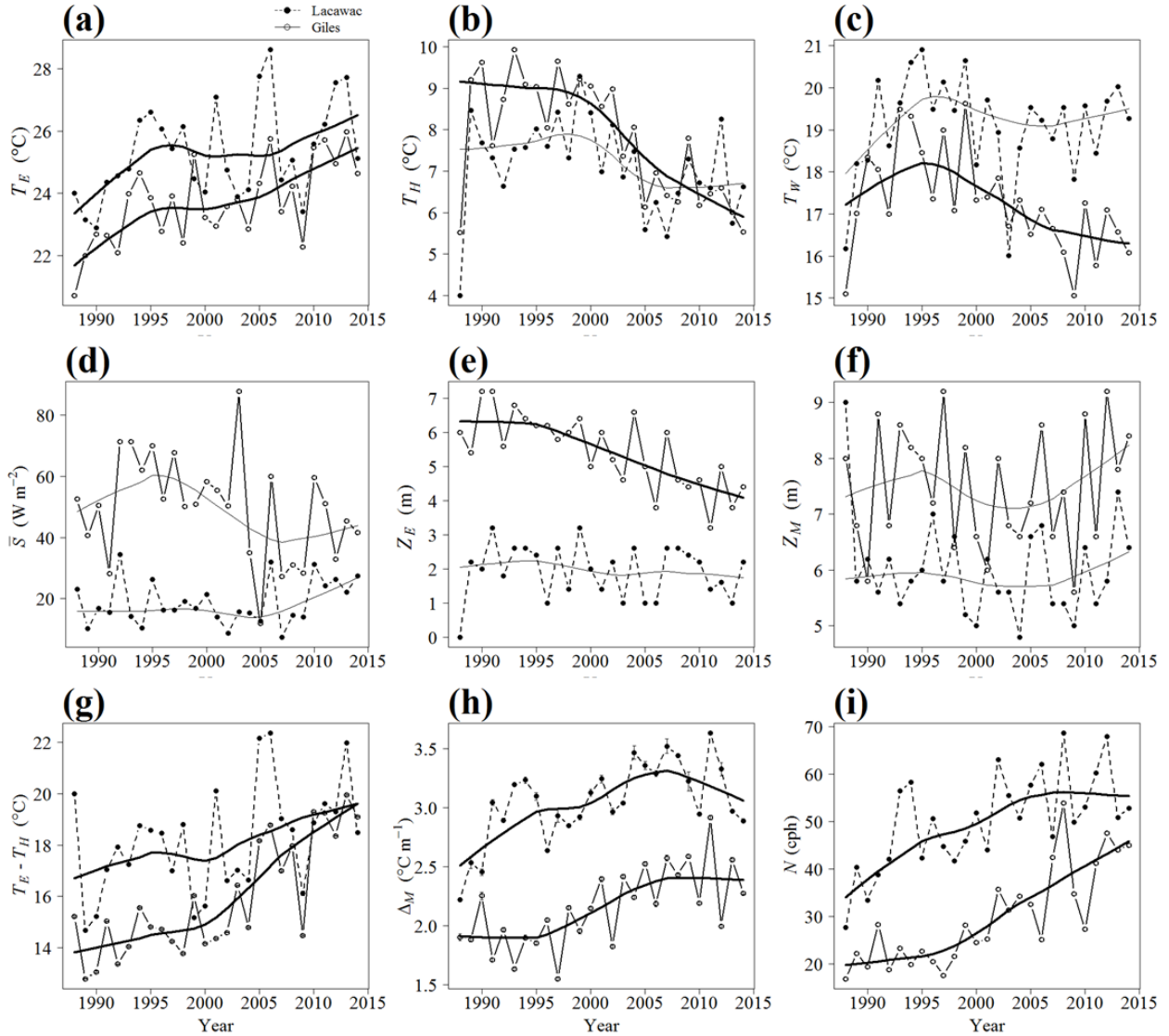
**Figure 2.** Mid-summer temperature profiles for (a) oligotrophic Lake Giles and (b) dystrophic Lake Lacawac averaged over the earliest five years (1988-1992, red) and the most recent five years (2010-2014, blue). Horizontal error bars represent  $\pm 1$  standard error of the mean at each depth. (c) Temporal trends of annually-averaged daily mean air temperature (gray circles;  $p = 0.71$ ), along with daily maximum (black circles;  $p = 0.68$ ) and minimum air temperature (open circles;  $p = 0.26$ ) in the study region. Trend lines in (c) are 15-year LOWESS smoothed trends.



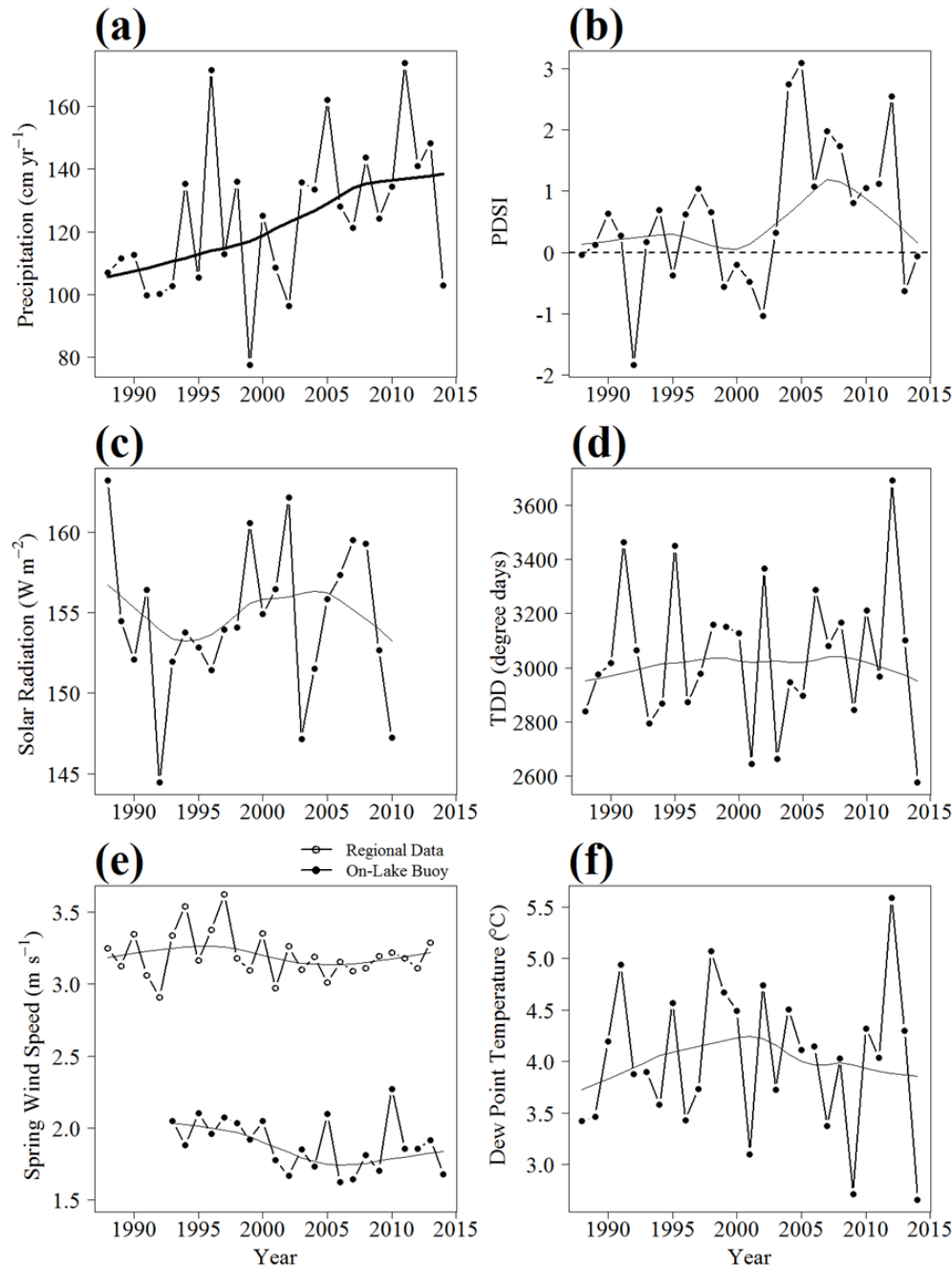
**Figure 3.** Water temperature vs. depth plots from high frequency thermistor data (10- to 60-minute readings) for 2 lake years: Lacawac 2012 (a, b) and Giles 2014 (c, d). Bold vertical lines in (a, c) represent the bounds of the July sampling window, the earliest and latest profiles used across the 27-year study period. Dashed vertical line represents the single profile used for the lake in the given year. Dashed horizontal line in (a) at 12 m represents the maximum depth for Lacawac. Black lines in (b, d) represent the mean temperature over the sample window for the given lake year. Error bars represent  $\pm 1$  standard deviation (thick line) and  $\pm 2$  standard deviations (thin line). Red lines represent the temperature readings at each depth of the single BIC profile. Note that all figures share the same depth and temperature scales.



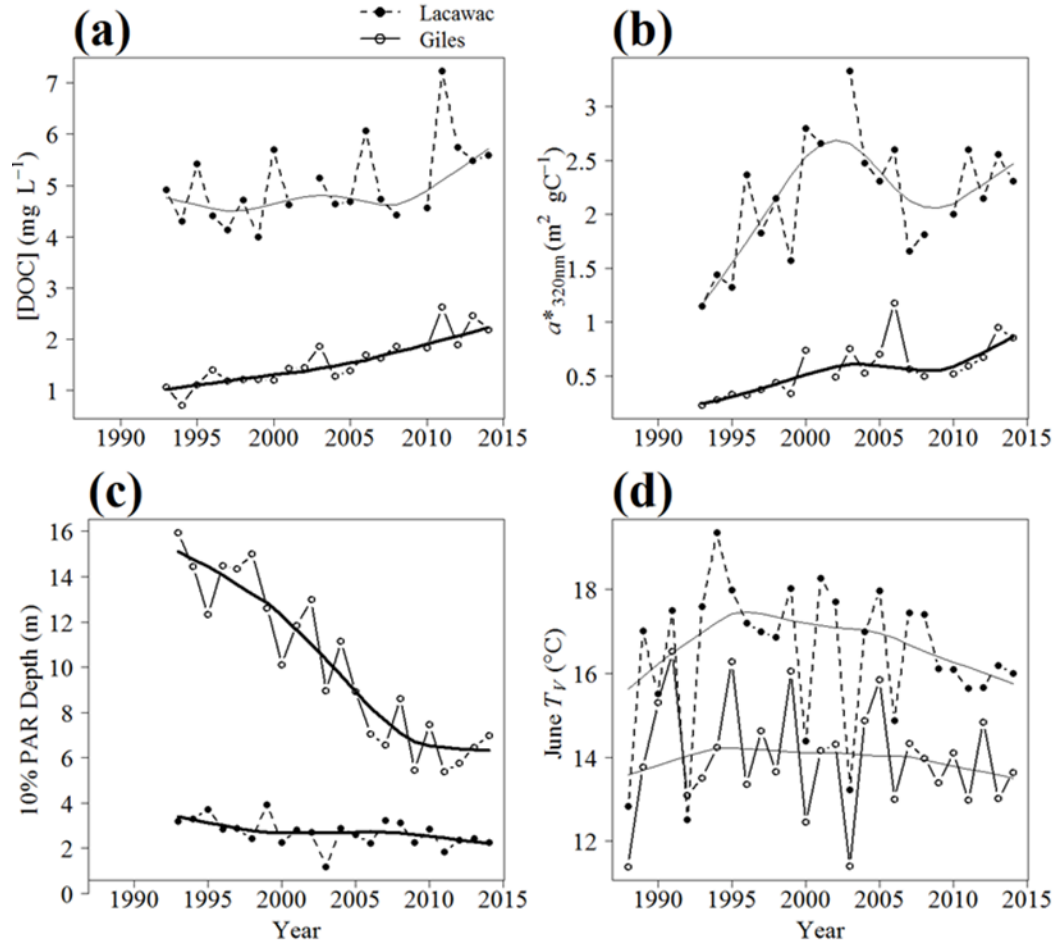
**Figure 4.** Temporal trends of lake thermal response metrics at Lake Lacawac (filled circles, dashed line) and Lake Giles (open circles, solid line) from non-parametric Mann-Kendall trend tests (for Lacawac and Giles, respectively). (a)  $T_E$  ( $p = 0.03$ ,  $p < 0.001$ ); (b)  $T_H$  ( $p = 0.06$ ,  $p < 0.001$ ); (c)  $T_W$  ( $p = 0.90$ ,  $p < 0.01$ ); (d) Mid-June to mid-July  $\bar{S}$  ( $p = 0.56$ ,  $p = 0.07$ ); (e)  $Z_E$  ( $p = 0.46$ ,  $p < 0.0001$ ); (f)  $Z_M$  ( $p = 0.60$ ,  $p = 0.92$ ); (g)  $T_E - T_H$  ( $p = 0.04$ ,  $p < 0.0001$ ); (h)  $\Delta_M$  ( $p < 0.001$ ,  $p < 0.0001$ ); (i)  $N$  ( $p < 0.001$ ,  $p < 0.0001$ ). Trend lines are 15-year LOWESS smoothed trends, with bold lines representing statistically significant Mann-Kendall trend tests. See Table 1 for abbreviations.



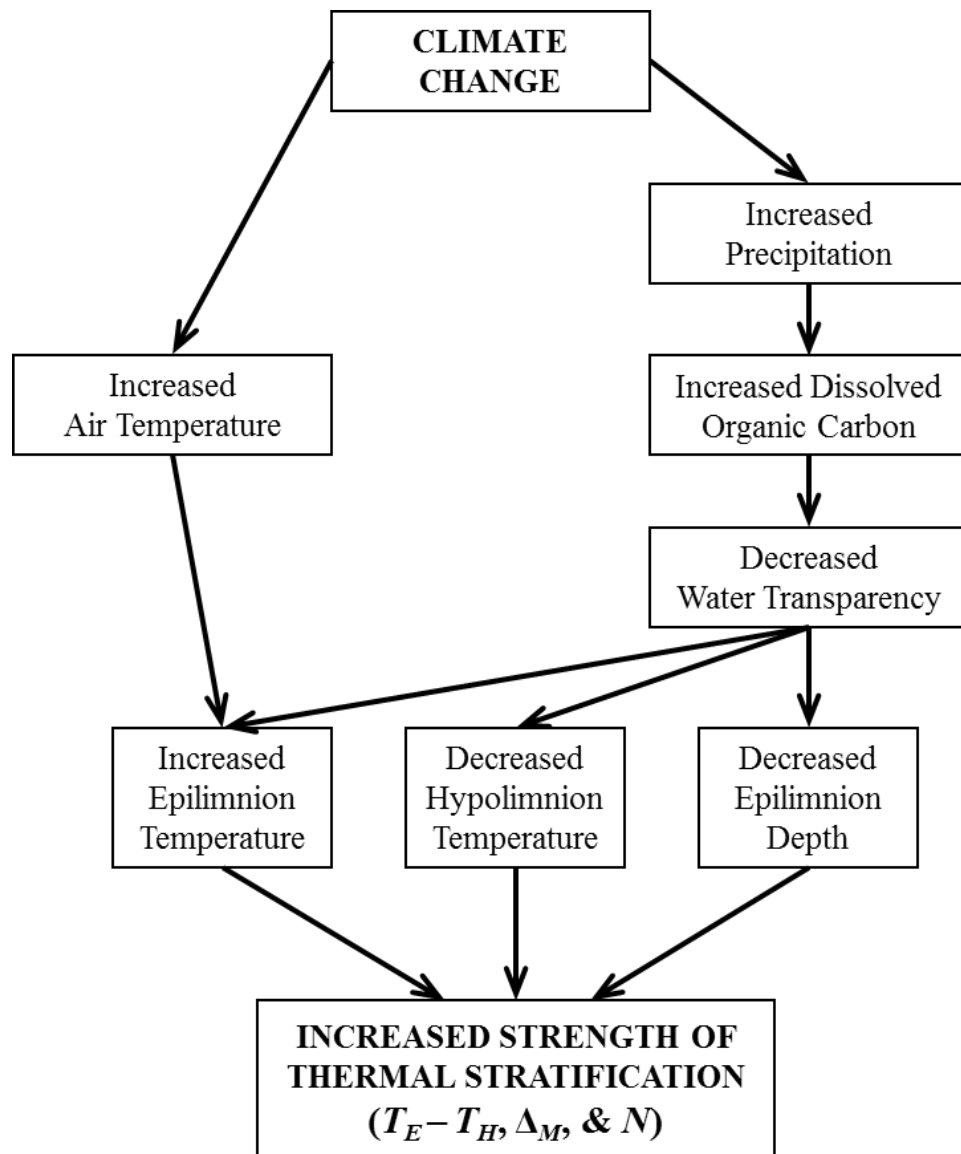
**Figure 5.** Temporal trends of meteorological variables in the study. (a) Annual precipitation ( $p = 0.01$ ); (b) Annually-averaged monthly PDSI ( $p = 0.07$ ); (c) Annually-averaged daily solar radiation ( $p = 0.60$ ); (d) Thawing degree days ( $p = 0.65$ ); (e) Monthly-averaged spring wind speed (regional mean  $p = 0.66$ , open circles; on-lake mean  $p = 0.09$ , closed circles); (f) Annually-averaged dew point ( $p = 1$ ). Trend lines are 15-year LOWESS smoothed trends, with bold lines representing statistically significant Mann-Kendall trend tests. Dashed line in (b) at zero represents neutral drought conditions.



**Figure 6.** Temporal trends of summer water transparency and heat content at Lake Lacawac (filled circles, dashed line) and Lake Giles (open circles, solid line), respectively. (a) Dissolved organic carbon concentration ( $p = 0.06$ ,  $p < 0.0001$ ); (b) DOC-specific absorbance,  $a^*$  ( $p = 0.11$ ,  $p < 0.001$ ); (c) 10% PAR depth ( $p = 0.02$ ,  $p < 0.0001$ ); (d) Volumetric whole-lake temperature from mid-June ( $p = 0.45$ ,  $p = 0.56$ ). Trend lines are 15-year LOWESS smoothed trends, with bold lines representing statistically significant Mann-Kendall trend tests.



**Figure 7.** Conceptual diagram outlining the proposed relationships between meteorological variables, lake thermal responses, and key linking factors in small, sheltered temperate lakes where wind is of negligible importance. Globally climate change is increasing air temperature, and in some regions is increasing precipitation, both of which lead to increased thermal stratification, but through different mechanisms. Other similar linkages may be important in other lake systems such as in the Arctic, where warmer air temperatures are increasing permafrost thaw and organic matter input to lakes (Cory et al. 2014).





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